

ALLOCRANGONYCTIDAE AND PSEUDOCRANGONYCTIDAE,
TWO NEW FAMILIES OF HOLARCTIC SUBTERRANEAN
AMPHIPOD CRUSTACEANS (GAMMARIDEA), WITH
COMMENTS ON THEIR PHYLOGENETIC AND
ZOOGEOGRAPHIC RELATIONSHIPS

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Abstract.—Two new families of gammaridean amphipod crustaceans, Allocrangonyctidae and Pseudocrangonyctidae, are described. The former is composed of a single genus that occurs in south-central United States; the latter is composed of two genera that occur in northeastern Asia. Members of both families inhabit subterranean freshwaters and are of stygobiont facies. Although the phylogenetic relationship of the allocrangonyctids is unclear, they are apparently allied with the genus *Pseudoniphargus* and may be aberrant hadzioids. The pseudocrangonyctids are allied with the Holarctic family Crangonyctidae and are assigned to the superfamily Crangonyctoidea.

The North American amphipod genus *Allocrangonyx* Schellenberg, and the east Asian genera *Pseudocrangonyx* Akatsuka & Komaï and *Procrangonyx* Schellenberg were originally assigned to the *Crangonyx* group of the old family Gammaridae (s.l.) by Schellenberg (1936). In recent years, however, the Gammaridae have been split into a number of separate families, and many of the genera placed in the *Crangonyx* group by Schellenberg have been assigned to different families. Some of these genera are now placed in the family Crangonyctidae (see Holsinger 1977, 1986a, b), with which *Allocrangonyx*, *Pseudocrangonyx* and *Procrangonyx* have sometimes been associated (see Bousfield 1983, Holsinger 1986a, b). Although these genera may be somewhat "crangonyctid-like" in overall similarity, they possess unique character state combinations that preclude their membership in this family (see Holsinger 1986a, b). Both *Allocrangonyx* and *Pseudocrangonyx/Procrangonyx* have been referred to informally as separate family groups by several workers (Bousfield 1977, 1978, 1982; Holsinger 1977, 1986b), but heretofore neither group

has been given formal family status. In this paper, I will show that each group represents a distinct family of gammaridean amphipods. Their phylogenetic, zoogeographic and super-familial relationships will also be examined.

Allocrangonyctidae, new family

Type genus (and only known genus).—*Allocrangonyx* Schellenberg, 1936.

Diagnosis.—Without eyes or pigment, of stygobiont facies. Body smooth except for few dorsal spines on uronites. Sexually mature male larger than female, with sexually dimorphic uropod 3. Interantennal lobe of head rounded anteriorly, inferior antennal sinus shallow. Antenna 1 longer than 2, accessory flagellum 2-segmented. Antennae lacking calceoli. Mandibles well developed; left lacinia mobilis 4-dentate; molar triturative; palp 3-segmented. Lower lip with thick inner lobes. Inner plate of maxilla 1 with one apical seta, outer plate with eight or nine unmodified (non-serrate/pectinate) apical spines. Apical margin of outer plate of maxilla 2 uneven (weakly bilobed), with two dis-

tinct sets of unequal setae; inner plate without oblique row of facial setae. Inner plate of maxilliped short, much smaller than outer; inner margin of outer plate with row of bladeliike spines.

Coxae 1–4 rather shallow, posterior margin of 4 weakly excavate. Propods of gnathopods powerful, subchelate, 2nd nearly twice size of 1st; palms bearing double row of tiny spines, many distally notched. Carpus (segment 5) of gnathopod 1 subequal in length to propod, that of gnathopod 2 proportionately much shorter. Pereopods 5–7 increasing in length posteriorly but otherwise generally similar; dactyls of 6 and 7 with several sets of anterior and posterior marginal spines. Coxal gill of gnathopod 2 large and bilobed; coxal gills of pereopods 3–6 ovate or subovate, with very short (rudimentary) stalks. Sternal gills absent. Brood plates sublinear. Distoposterior corners of pleonal plates not acuminate. Pleopods subequally biramous. Uronite 3 without ecdysial spine on ventral margin. Margins and apices of uropods 1 and 2 with spines, peduncle of 1 with basofacial spine. Uropod 3 elongate, biramous (parviramous); inner ramus greatly reduced (scale-like); outer ramus well developed, bearing tiny 2nd segment, becoming greatly elongate and secondarily segmented in larger males. Telson short, with shallow apical notch, apical lobes with spines.

Relationship.—In comparison with a number of potentially related outgroups of gammaridean amphipods, including the Crangonyctidae, Hadziidae, Niphargidae, Pseudocrangonyctidae (new family described below), and *Pseudoniphargus* (probable family group, but not formally named to date), the Allocrangonyctidae possess at least five, presumably autapomorphic, character states that, in full combination, make them unique: (1) large, bilobed coxal gill on gnathopod 2; (2) non-serrate (or non-pectinate) spines on apex of outer plate of maxilla 1; (3) stalks of coxal gills vestigial; (4) posterior marginal spines on dactyls of pereopods 6 and 7; and (5) positive allo-

metric growth in combination with secondary segmentation of outer ramus of male uropod 3.

Although the allocrangonyctids share a number of important characters with other genera, such as *Pseudoniphargus*, *Niphargus*, and members of the Crangonyctidae (see Holsinger 1971, Bousfield 1977, Barnard & Karaman 1980, Notenboom 1988), their phylogenetic relationship has never been clearly demonstrated. *Allocrangonyx* shares at least 14 apomorphic characters with the peri-Mediterranean, amphi-Atlantic subterranean genus *Pseudoniphargus* Chevreux (and its satellite genus *Parapseudoniphargus* Notenboom) (Table 1). At least seven of these characters are also shared with the western Palearctic subterranean genus *Niphargus* (characters 1, 3, 4, 6, 7, 10, 13) but there are also a number of important differences between this genus and *Allocrangonyx* (see Holsinger 1971, Notenboom 1988). In addition, five of these characters are shared with genera in the Holarctic family Crangonyctidae (characters 1, 8, 11, 13, 14), but character 8 of the crangonyctids may be different (i.e., the palmar spines are proportionately much larger), and character 11 is variable among species in several genera. Based on the significantly greater number of apomorphic characters shared by *Allocrangonyx* and *Pseudoniphargus*, the allocrangonyctids are obviously more closely related phylogenetically to the latter than they are to either *Niphargus* or the crangonyctid genera.

Allocrangonyx Schellenberg

Allocrangonyx Schellenberg, 1936:33 (type species by original designation, *Niphargus pellucidus* Mackin, 1935).—Holsinger, 1971:318–319.—Barnard & Barnard, 1983:447–448.

Remarks.—Many of the important characters of the genus are clearly stated in the literature (see above) and need not be repeated here. Some omissions and mistakes

in earlier descriptions should be pointed out, however. Segment 3 of the mandibular palp is heavily setose and bears A, B, C, D and E setae. Carpus of gnathopod 1 is relatively long, approximately as long as the propod; merus bears a small, semihyaline posterior lobe. Carpus of gnathopod 2 is short, less than $\frac{1}{2}$ the length of propod, and bears a distinct (narrow) posterior lobe. A majority of palmar margin spines on the gnathopods in the outer row are distally notched and not simply "spinate" or setule tipped as indicated by Holsinger (1971). Coxal gills (on pereopods 3–6) have vestigial peduncles or stalks. Coxal gill 1 shown by Barnard & Barnard (1983:211, fig 9I) is mislabelled a sternal gill. The small basofacial spine on peduncle of uropod 1 was inadvertently omitted on plate 107 (fig. 4m) in Holsinger (1971) and also in the diagnosis by Barnard & Barnard (1983:448). Uropod 3 of the male shown in Holsinger (1986a:540, fig. 1) is drawn too short; it should be about twice as long as indicated.

At present the genus is composed of two troglobitic species from south-central United States, the geographic distributions of which are shown on a number of range maps (see Holsinger 1971, Barnard & Barnard 1983, Holsinger 1986a, b). The distributions shown in Holsinger (1986b, fig. 6) encompass all known localities recorded to date, including those given below.

Allocrangonyx pellucidus (Mackin)

Fig. 1

Allocrangonyx pellucidus (Mackin).—Holsinger, 1971:320–322 (with references).—Black, 1971:7.—Holsinger, 1972:77, fig. 32b.—Black, 1973:15.—Reisen, 1975:28, 30.—Pennak, 1978:460, fig. 317H, K.—Barnard & Barnard, 1983:447–448, fig. 18D.—Fitzpatrick, 1983:151.—Holsinger, 1986a:540, 542, fig. 1; 1986b:97.

Range.—Caves and springs of the Arbuckle Mountains in south-central Oklahoma (Murray and Pontotoc counties).

Table 1.—List of 14 apomorphic character states shared by *Allocrangonyx* and *Pseudoniphargus/Parapseudoniphargus*. Outgroups used to determine character polarity include: Crangonyctidae, Gammaridae, Hadziidae, Niphargidae and Pseudocrangonyctidae.

1. Accessory flagellum of first antennae 2-segmented.
2. Lacinia mobilis of left mandible 4-dentate.
3. Lower lip with thick inner lobes.
4. Apical setae of inner plate of maxilla 1 reduced in number (typically less than 3) and often non-plumose, or only weakly so.
5. Apical margin of outer plate of maxilla 2 uneven and bearing two distinct groups of setae.
6. Inner plate of maxilla 2 without oblique row of facial setae.
7. Inner plate of maxilliped reduced in size relative to outer plate.
8. Distally notched spines on palms of gnathopod propods.
9. Merus of gnathopod 1 with posterior lobe (sometimes semihyaline, sometimes pubescent).
10. Absence of sternal gills.
11. Brood plates narrowly sublinear.
12. Peduncle of uropod 1 with basofacial spine.
13. Inner ramus of uropod 3 reduced to scalelike plate.
14. Telson relatively short and not deeply notched or cleft (lobes nearly completely fused).

New locality record (since Holsinger 1971) based on material in author's collection.—Oklahoma, Murray County: spring on Honey Creek near Davis (W. K. Reisen, collector).

Allocrangonyx hubrichti Holsinger

Figs. 2, 3

Allocrangonyx hubrichti Holsinger, 1971: 324–326, pls. 107–109 (with references).—Holsinger, 1972:77–78, fig. 32a.—Pflieger, 1974:36.—Craig, 1975:4; 1977:83.—Nordstrom et al., 1977:8.—Barnard & Barnard, 1983:447–448, fig. 9I.—Fitzpatrick, 1983:151.—Wilson, 1984:26.—Gardner, 1986:17–18.—Holsinger, 1986a:542; 1986b:97.

Range.—Caves and spring(s) of the Ozark Plateau in east-central Missouri (Phelps, Pulaski and Washington counties).

New locality records (since Holsinger

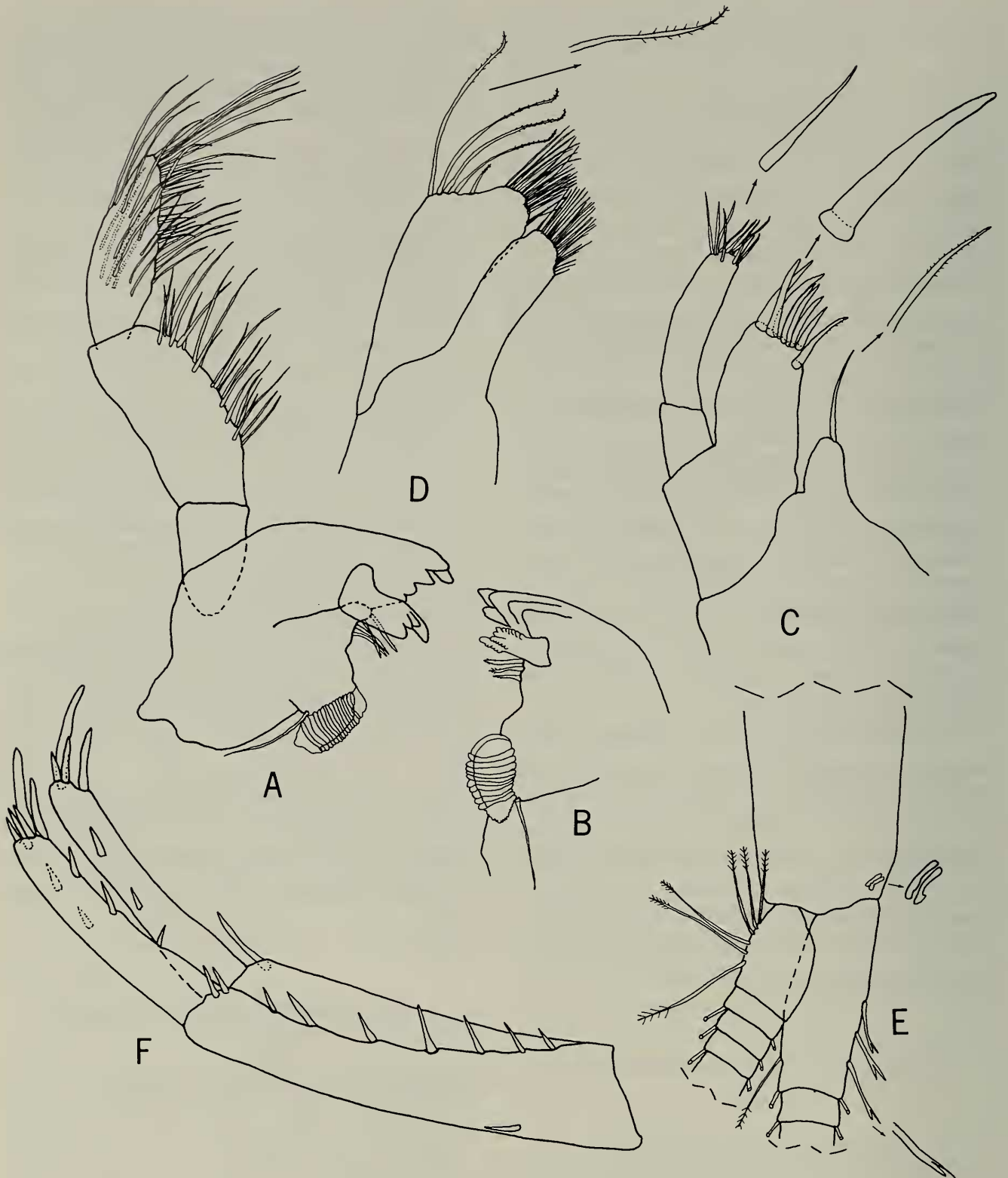


Fig. 1. *Allocrangonyx pellucidus* (Mackin). Male (21.75 mm), seep, 0.5 km NW of Turner Falls, Murray County, Oklahoma: A, Left mandible; B, Dentate part of right mandible; C, Maxilla 1; D, Maxilla 2. Maxillae drawn to larger scale than mandibles. Female (18.00 mm) from same locality: E, Pleopod 1 (in part), F, Uropod 1.

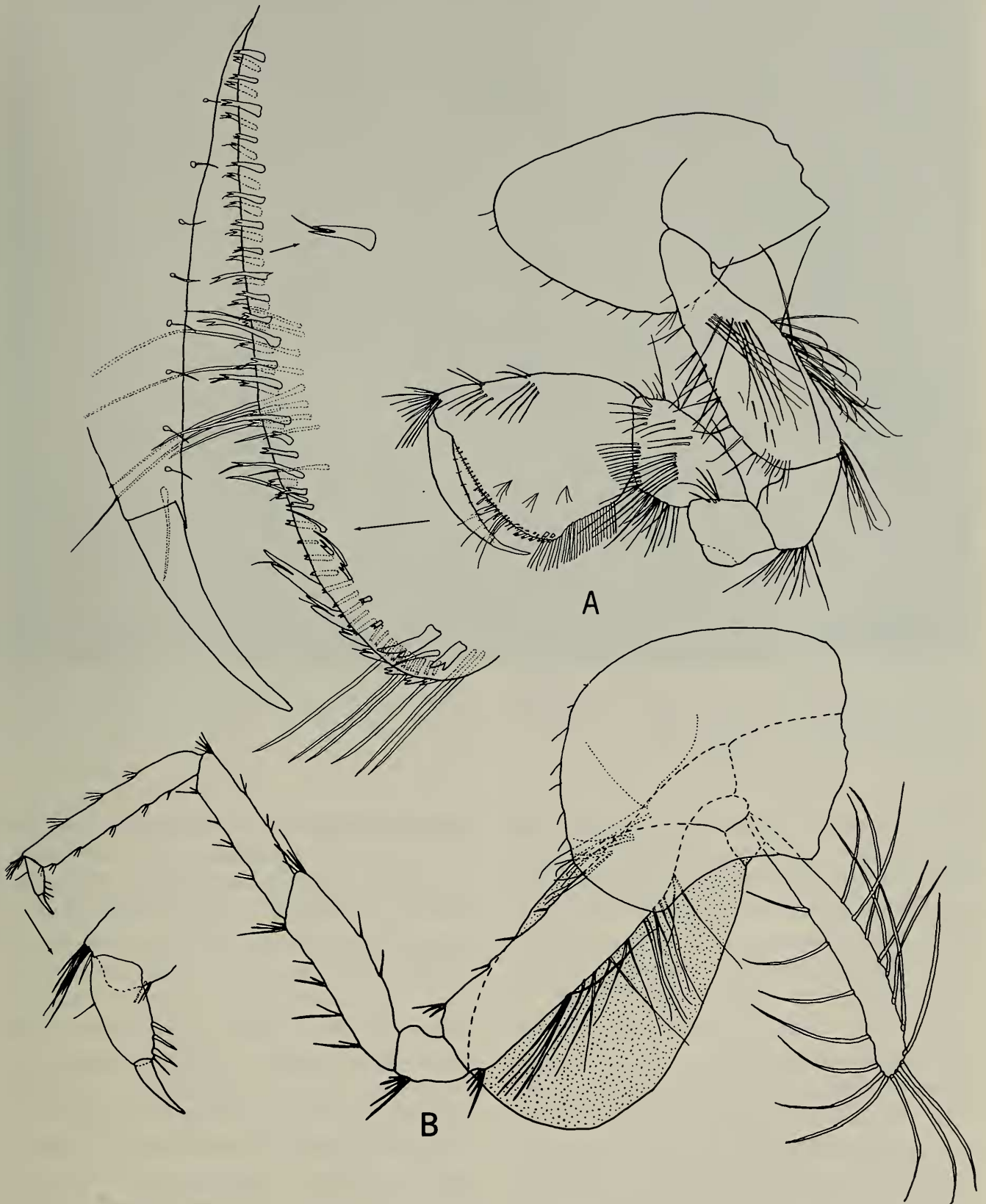


Fig. 2. *Allocrangonyx hubrichti* Holsinger. Female (17.00 mm), Saltpeter Cave, Phelps County, Missouri: A, Gnathopod 1 (palm enlarged); B, Pereopod 4 (dactyl enlarged). Gnathopod and pereopod drawn to same scale.

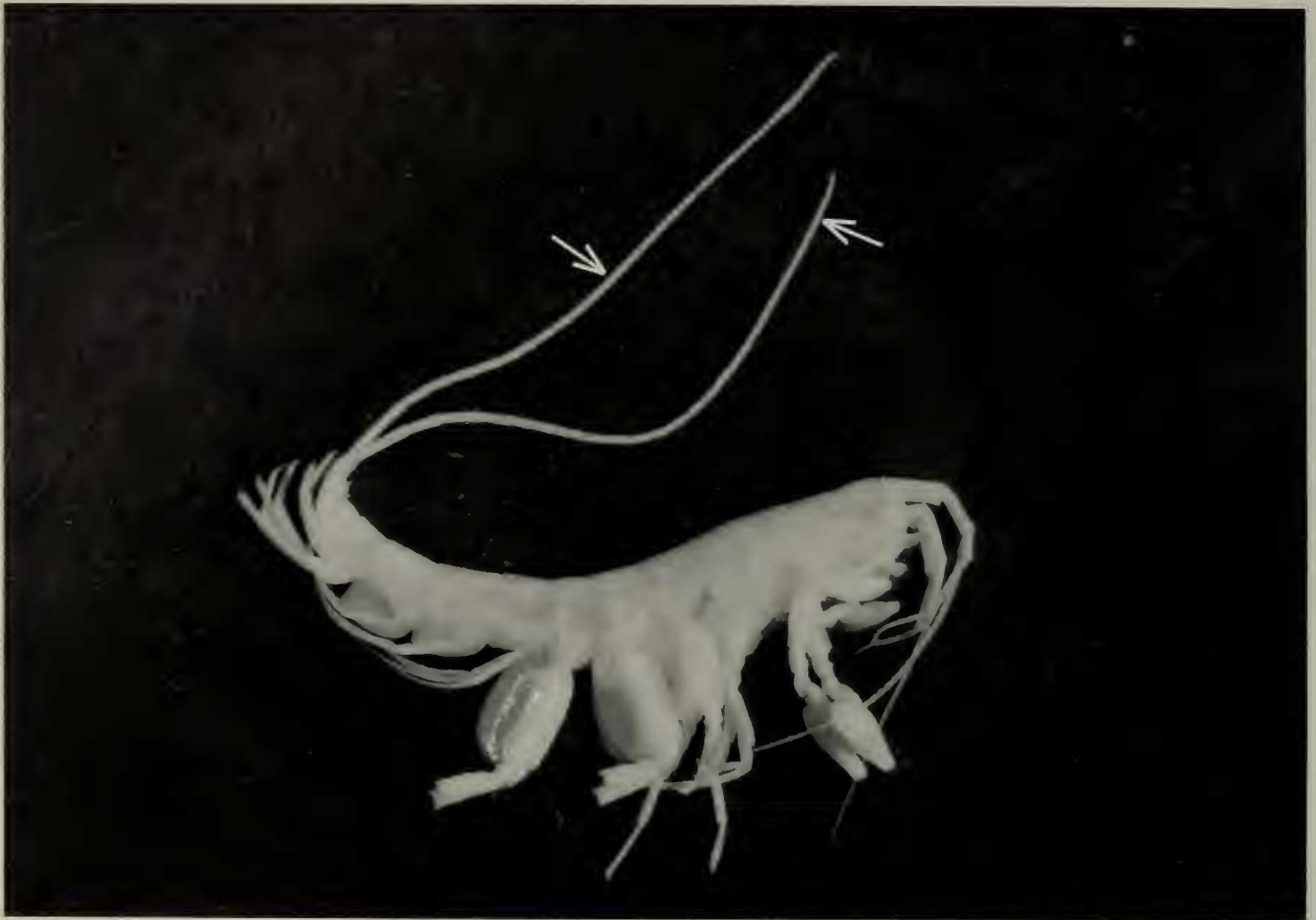


Fig. 3. Male specimen (16.0 mm) of *Allocrangonyx hubrichti* Holsinger from Kaintuck Hollow Natural Bridge, Phelps County, Missouri. Elongate 3rd uropods indicated by white arrows. Note that last three segments of pereopods 6 and 7 are broken off.

1971); based on material in author's collection).—Missouri, Phelps County: Kaintuck Hollow Natural Bridge (in stream pool), 18 km SW of Rolla (J. E. Gardner, coll.).—Meramec Spring, 8 km SE of St. James (J. E. Gardner, coll.). Pulaski County: Killam Cave (in pool), 14 km S of Waynesville (J. E. Gardner, coll.). Washington County: Hamilton Springs Cave (in pool), 12 km SE of Sullivan (J. L. Craig and T. Cravens, coll.).—Mossy Spring Cave (in stream), 16 km E of Richwoods (J. E. Gardner, coll.).

Remarks.—The remarkable developmental changes in the third uropod of both species of *Allocrangonyx* were discussed at some length by Holsinger (1971). During growth, the second segment of the outer ramus decreases in proportion to an increase in size of the first segment in both sexes. In males, the first segment of the outer ramus

increases allometrically in relation to both the length of the peduncle and the body and, in concert with increase in size, the outer ramus differentiates into secondary segments. This unusual secondary sexual dimorphism is even more pronounced in *A. hubrichti*. For example, as reported earlier (Holsinger 1971, 1972) uropod 3 was 45% as long as the body, with 9 secondary segments, in a 15.0 mm-long male, and 65% as long as the body, with 16 secondary segments, in a 18.0 mm-long male. In a more recently collected male specimen, 16.0 mm in length, uropod 3 was as long (or slightly longer) than the body, with 30 secondary segments (see Fig. 3).

Elongation of uropod 3 in larger males of many species *Pseudoniphargus* has also been reported (Stock 1980). But in this genus, the peduncle may also become elongate and the

outer ramus neither differentiates into secondary segments nor reaches the extraordinary length seen in *A. hubrichti* (Stock 1980, Notenboom 1986, 1988). Although there are no observations on the reproductive behavior of these organisms, the possibility that the hyperextended third uropod of the male of *Allocrangonyx* is utilized either in sex recognition or manipulation of the female during copulation, or even agonistic behavior between males, should be investigated.

Pseudocrangonyctidae, new family

Type genus.—*Pseudocrangonyx* Akatsuka & Komai, 1922.

Diagnosis.—Typically without eyes (except one species) and pigment, of stygobiont facies. Body generally smooth, except last seven body segments bearing dorsal setae and uronite 2 bearing few small dorsal spines. Sexually mature females larger than males. Interantennal lobe rounded anteriorly, inferior antennal sinus shallow. Antennae 1 longer than 2, accessory flagellum 2-segmented. Antennae without calceoli. Apical margin of upper lip rounded, unnotched. Mandibles well developed; molar weakly tritulative, bearing single seta or not; left lacinia mobilis 5-dentate; segment 3 of palp equal in length to segment 2, with A (sometimes), D and E setae. Inner lobes of lower lip small or vestigial. Inner plate of maxilla 1 with apical plumose setae, outer plate with typically seven serrate (or pectinate) spines. Inner plate of maxilla 2 with oblique row of facial setae. Inner margin of outer plate of maxilliped with setae and few small spines, but lacking bladespines.

Coxae shallow, barely touching or typically discontinuous; posterior margin of 4 without excavation. Propods of gnathopods relatively large (crangonyctid-like), subchelate; propod of 1 a little larger than 2; palms rather long, oblique, armed with double row of distally notched spines (possibly variable). Carpus of gnathopod 1 short, with

small posterior lobe; that of 2 longer, without lobe. Pereopods 3 and 4 normal, subequal in length. Pereopods 5–7 increasing in overall length posteriorly; bases with small distoposterior lobes. Stalked coxal gills on gnathopod 2 and pereopods 3–6. Single median sternal gills on pereonites 2–4 or 2–5. Brood plates small, sublinear. Distoposterior corners of pleonal plates not acuminate. Pleopods normal, subequally biramous; peduncles with 2 coupling spines each. Uropods 1 and 2 biramous, with marginal and apical spines; peduncle of 1 with basofacial spine(s). Uropod 3 uniramous; ramus elongate, bearing spines and few setae, 2nd segment present and short, or absent. Telson longer than broad; apical margin with notch of variable depth but typically rather shallow (not deeper than the 1/2 length of telson); apical lobes with few spines.

Remarks.—At present this family is composed of two northeast Asian genera, *Pseudocrangonyx* and *Procrangonyx*. Their geographic distribution is shown on maps in Barnard & Barnard (1983) and Holsinger (1986b). Unfortunately, previous descriptions of taxa assigned to this family have been very uneven. Thus important taxonomic details are available for some species (e.g., *Pseudocrangonyx asiaticus* and *P. coreanus*) but are lacking or unclear for others (e.g., *Procrangonyx* and other species of *Pseudocrangonyx*). It may therefore be necessary to amend the family diagnosis given above as these missing taxonomic details become available.

Relationship.—Although the Pseudocrangonyctidae are allied with the Holarctic family Crangonyctidae as indicated below, they differ from this group in a number of important characters and warrant recognition as a distinct family: (1) segment 3 of mandibular palp equal in length to segment 2; (2) molar of mandible weakly tritulative (or perhaps not tritulative in some species); (3) gnathopods and pereopods tending to be more setose, especially segment 2 (basis) of the gnathopods and pereopods 3 and 4, and

the coxae of pereopods 5–7; (4) coxae generally discontinuous (a character shared with many members of the family Bogidiellidae); (5) abdominal segments (pleonites and uronites) and 7th pereonite with clusters of setae dorsodistally; (6) uronites with small spines (1st with ecdysial spine on ventral margin, 2nd with few dorsodistal spines, 3rd with several spines ventrodistally near base of peduncle of uropod 3); and (7) uropod 3 uniramous and elongate, with ramus 3 to 6 times length of peduncle.

A relatively close phylogenetic relationship between the families Pseudocrangonyctidae and Crangonyctidae is indicated by similarity of the following characters, most of which are apparently synapomorphies: (1) 2-segmented accessory flagellum; (2) structure of mouthparts, except that mandibular palp segment 3 is proportionately a little longer and the molar is not as strongly developed in the Pseudocrangonyctidae (see above); (3) similar shape of, and proportionately large, gnathopod propods (in combination with short carpi); (4) palms of gnathopod propods with double row of thick, distally notched spine teeth (although possibly variable in Pseudocrangonyctidae); (5) rastellate setae on carpus of one or both gnathopods; (6) median sternal gills; (7) loss of inner ramus of uropod 3 (cf. *Stygobromus* and *Synurella*); and (8) relatively short telson with shallow apical notch (variable).

Pseudocrangonyx Akatsuka & Komai

Pseudocrangonyx Akatsuka & Komai, 1922: 120 (type species not designated therein).—Uéno, 1966:504–505 (with references).—Barnard & Barnard, 1983:442–443 (type species *Pseudocrangonyx shikokunis* Akatsuka & Komai, designated therein).

Remarks.—Nine species are included in this genus at present; detailed range maps are found in Birstein (1955), Uéno (1966) and Barnard & Barnard (1983). They in-

habit subterranean waters (e.g., caves, springs, wells) in northeastern China, eastern Siberia (including the Kamchatka Peninsula), Korea and the Japanese Islands (see Holsinger 1986a). Further details on one of these species are given below.

Pseudocrangonyx asiaticus Uéno

Fig. 4

Pseudocrangonyx asiaticus Uéno.—Uéno, 1966:506–518, figs. 2–8 (with references); 1971:198.—Barnard & Barnard, 1983:443, figs. 8B, 9G, 11B, 18C, 20A.—Holsinger, 1986a:542, fig. 4.

Material examined.—South Korea: Gosulgul (cave), 2 males collected by B. A. Lee (in Zoölogisch Museum of Amsterdam collection); Simbog-gul (cave) (location in Uéno 1966:502–503), 12 females, 6 males, 1 juv. collected by K. S. Lee (in author's collection).

Range.—Subterranean waters in Korea, northeastern China and the Tsushima Islands of Japan.

Remarks.—Although Uéno's (1966) re-description of this species (and also the description of *P. coreanus* in the same paper) was very thorough, my recent examination of the above material revealed some taxonomic details that were either omitted or should be further emphasized as follows.

Segment 3 of mandibular palp equal in length to segment 2, bearing several short A setae on outer margin, row of short D setae on distal half of inner margin, and 7 to 8 longish E setae of unequal length on apex. Mandible: molar weakly triturative, bearing 1 seta; left lacinia mobilis 5-dentate. Dactyls of gnathopods with row of blade-like processes (spines?) on inner margin; ungues relatively long. Propod of gnathopod 1: palm with uneven double row of distally notched spine teeth and row of long setae on outside; medial setae present, in sets of 2s and 4s. Propod of gnathopod 2: palm with double row of 5 distally notched spine teeth; defining angle with 2 spine teeth on

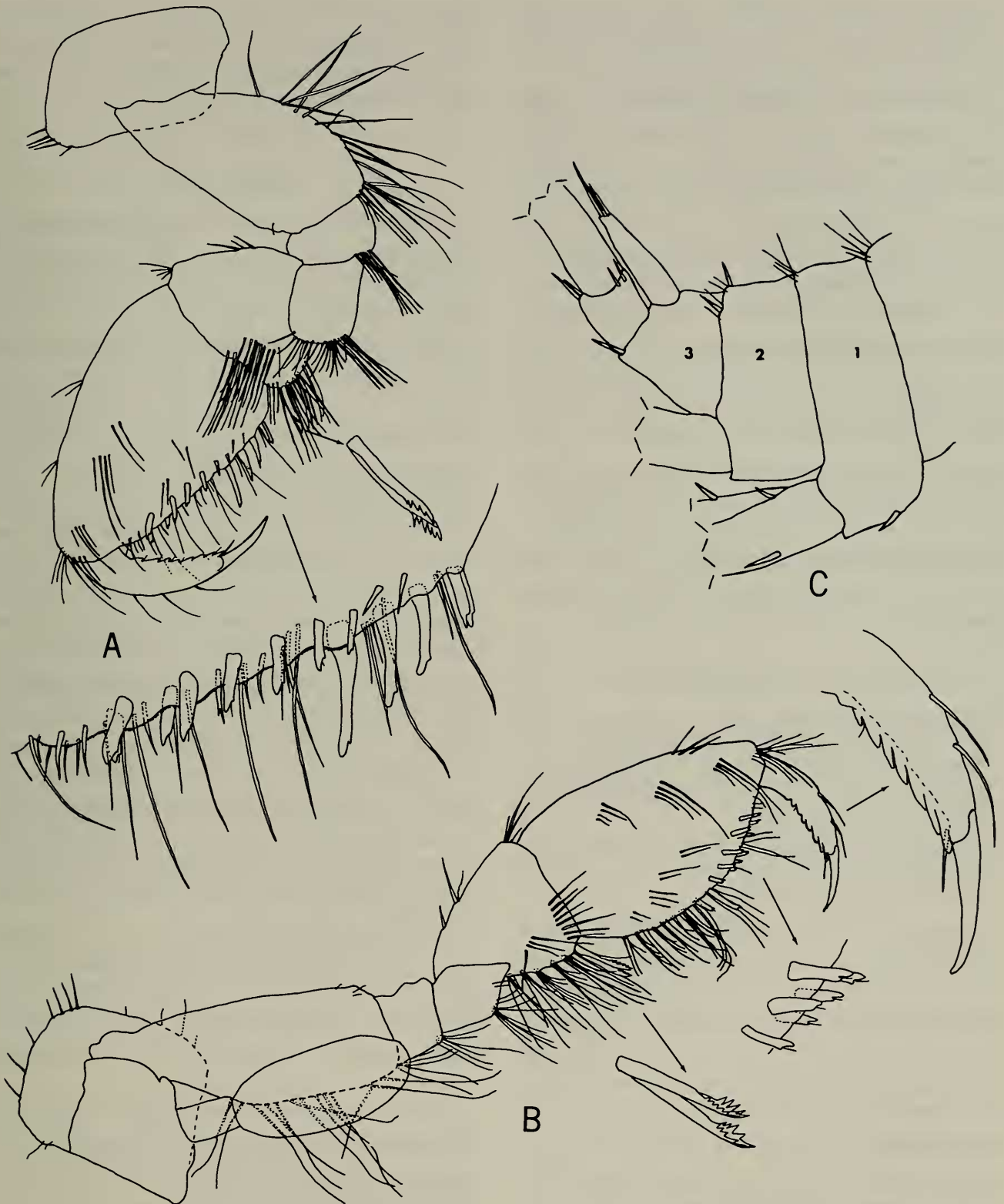


Fig. 4. *Pseudocrangonyx asiaticus* Uéno. Female (10.2 mm), Simbog-gul (cave), South Korea: A, Gnathopod 1 (rastellate setae and palmar margin enlarged); B, Gnathopod 2 (dactyl, palmar spines and rastellate setae enlarged). Male (6.9 mm) from same locality: C, Urosome (uronites 1, 2, 3) (Gnathopods and urosome drawn to same scale.)

outside; inferior medial setae in sets of mostly 2s, superior medial setae in sets of 4s. Segment 5 of gnathopods bearing 2 rastellate setae on posterior margin at distal end. Pereonites 5–7 with sternal blisters (small ventral humps) (cf., *Sternophysinx* from South Africa and species of the *hubbsi* group of *Stygobromus* from western United States). Upper half of posterior margins of pleonites (of larger specimens) with short row of fine setae. Pereonite 7 and abdominal segments each with cluster of 4 to 8 fine setae dorsodistally. Uronite 1 with ecdysial spine(s) on ventral margin, uronite 2 with 2 short spines dorsodistally, uronite 3 with few spines ventrodistally near base of peduncle of uropod 3. Uropod 2 of male sexually dimorphic: inner ramus with 2 or 3 distally serrate, apical spines in cluster with several unmodified spines (sexually mature females lack modified apical spines).

Procrangonyx Schellenberg

Procrangonyx Schellenberg, 1934:217 (type species by monotypy, *Eucrangonyx japonicus* Uéno, 1930).—Barnard & Barnard, 1983:444–445.

Eocrangonyx Schellenberg, 1936:37 (objective junior synonym).

Remarks.—*Procrangonyx* is based on a single species, *P. japonicus*, which was described by Uéno (1930) from two male specimens taken from a subterranean stream in the suburbs of Tokyo (see also Holsinger 1977, 1986a). Except for the absence of a 2nd segment on the ramus of uropod 3, this genus appears to be closely allied with *Pseudocrangonyx*. However, Uéno's original description was incomplete, and several important taxonomic details were omitted or are unclear. For example, it cannot be determined from the description whether the palmar margin spines of the gnathopod prolegs are distally notched or not.

Although Uéno (1930) stated that the type specimens were deposited in the collection of the Otsu Hydrobiological Station, my at-

tempts to borrow this material or further study have been unsuccessful. Unfortunately, there is a good possibility that the type specimens no longer exist.

Discussion

Both mosaic evolution and convergence are common phenomena in the Amphipoda and have resulted in many taxa that are difficult to interpret phylogenetically or to classify with any degree of certainty. Numerous taxa display mosaic patterns, resulting from differential rates of evolution and reflected in curious mixtures of plesiomorphic and apomorphic characters. In many instances a single taxonomically important structure, such as the gnathopod or uropod 3, may display a combination of both primitive and advanced character states. Convergence has led to the evolution of homoplastic structures in taxa that otherwise are apparently only distantly related. Frequently, these homoplasies involve lost or reduced structures (e.g., one or both rami of uropod 3) that are often difficult to interpret cladistically. For these reasons there has been considerable confusion regarding the phylogenetic relationship of the allocrangonyctids with other families of gammaridean amphipods, as well as their placement in a superfamily that most clearly reflects their taxonomic affinities. It is doubtful if morphology alone can ever provide a wholly satisfactory solution to this problem.

Because of their morphological similarity and potential relationship to *Niphargus*, *Allocrangonyx* and *Pseudoniphargus* were originally aligned in a single, unnamed family group and assigned to the superfamily Niphargoidea by Bousfield (1977, 1978). Barnard & Karaman (1980:13), however, suggested that these two genera "only have in common a few coincidental characters" and therefore should not be assigned to the same family group. They also strongly advocated abandoning the superfamily Ni-

phargoidea and suggested placing both *Pseudoniphargus* and the niphargids in the superfamily Hadzioidea. Subsequently, Bousfield (1982) reassigned *Allocrangonyx* to the superfamily Crangonyctoidea and also suggested that *Pseudoniphargus* is more closely allied to the superfamily Melitoidea (=Hadzioidea). In their treatise "Freshwater Amphipoda of the World," Barnard & Barnard (1983) referred to the "allocrangonyctids" as a member of their "Sternobranchiate Groups (Crangonyctoids)," but they did not propose any formal taxonomic designation.

Despite significant differences in geographic distribution and ecology, which are pointed out below, the allocrangonyctids are probably more closely related phylogenetically to the pseudoniphargids than to any other group of amphipods. Although several workers, including Stock (1980), Barnard & Karaman (1980), and Notenboom (1988), attribute much of the similarity between these two groups to convergence (homoplasy) or as being overvalued, I believe that the high number of apomorphic characters they share suggests otherwise. It is unlikely that so many detailed similarities in the mouthparts and gnathopods of these genera would have resulted from convergence.

The geographic distribution of *Allocrangonyx* is restricted to subterranean freshwaters in the central interior of North America and is far removed from coastal areas at present. Its range does not extend into areas exposed to marine embayments in the Tertiary or even the Cretaceous, but a part of it in southern Oklahoma would have been less than 100 kilometers from marine embayments in the Late Cretaceous (Holsinger 1971). This distribution pattern suggests that *Allocrangonyx* represents a relict lineage, long removed from marine ancestors. In contrast, species of *Pseudoniphargus* occupy a wide range of marine to fresh water, subterranean habitats in the circum-Mediterranean region of southern Eu-

rope and North Africa and on several islands in the Atlantic, including the Azores, Madeira and Bermuda (Stock 1980; Stock et al. 1986; Notenboom 1986, 1987a, b, 1988). These species occur at present in coastal areas or in areas that were directly exposed to marine embayments in the Tertiary.

Neither the difference in geographic distribution between *Allocrangonyx* and *Pseudoniphargus*, nor the fact that some species of the latter live in brackish (or even marine) water, rule out the origin of these two groups from a common ancestor, however. The many synapomorphies between these groups indicate a common ancestry. On this basis, I suggest that the allocrangonyctid and pseudoniphargid lineages could have been derived from a widespread ancestor that inhabited the old Tethyan seaway in Mesozoic times. At that time the areas presently occupied by these groups would have been much closer geographically. Subsequent continental movements combined with widening of the Atlantic, regression of shallow inland seas, and various other geological changes would have severely isolated these groups from each other. Divergence during the long period of geographic isolation that followed has produced some major morphological differences, but enough important similarities remain to support an obvious phylogenetic relationship.

Notenboom (1988) has recently pointed out a number of important similarities, presumably synapomorphies, between *Pseudoniphargus* and the monotypic genus *Allomelita*, which occurs in brackish waters and sometimes in interstitial habitats along the coast of Europe from Norway to Portugal. *Allomelita*, in turn, is closely allied with *Melita* and is thus a bona fide member of the superfamily Hadzioidea as presently understood. The cladistic relationship between *Allocrangonyx* and *Pseudoniphargus* is certainly as strong as that of the latter with *Allomelita*, suggesting, ipso facto, that both the allocrangonyctids and pseudoni-

phargids may also be members of the Hadzioidea. Although some problems regarding the phylogenetic affinities of *Allocrangonyx* and *Pseudoniphargus* remain unresolved, there is a good possibility that both are highly divergent hadzioids. Their morphological character combinations make it highly improbable that either is a crangonyctoid or niphargoid as some workers have previously suggested.

The phylogenetic relationship of the family Pseudocrangonyctidae is less problematic. The number of apomorphies shared by this family and the Crangonyctidae suggest a relatively close phylogenetic relationship of these two groups. These two families, in turn, can be placed in the superfamily Crangonyctoidea, which by definition also includes the freshwater families Neoniphargidae and Paramelitidae of the Southern Hemisphere (see Bousfield 1978, 1982, 1983; Holsinger 1986a, b; Williams & Barnard 1988).

Both the pseudocrangonyctids and crangonyctids are known only from freshwater habitats in the Northern Hemisphere and lack close morphological affinities with any group of marine amphipods. They are therefore believed to represent very old groups of freshwater amphipods that originated on the Laurasian paleocontinent prior to the separation of Eurasia and North America (Holsinger 1986a, b). Geographically, the pseudocrangonyctids replace the crangonyctids in extreme eastern Asia, where the latter are almost entirely absent (see Holsinger 1986b:fig. 1). The present range of *Pseudocrangonyx*, which encompasses parts of the northeastern Asian mainland and the Japanese Islands, probably reflects an earlier, continuous distribution of this genus in freshwater habitats throughout the region. Separation of the Japanese Islands as slivers from the Asian continent by tectonic activity beginning in the middle Tertiary (see Dott & Batten 1976) would have isolated populations in Japan from those on the mainland. Based on the assumption that

Pseudocrangonyx is an old subterranean freshwater inhabitant, it is highly unlikely that any of these insular populations were established by recent invasions from marine waters.

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